Functional Ecology

The return of the trophic chain: fundamental vs realized interactions in a simple arthropod food web

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ITC collected the data;

JML, MM, and ITC analysed the data;

MM and SM led the writing of the manuscript.

All authors contributed critically to the drafts and gave final approval for publication.

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Abstract

1. The mathematical theory describing small assemblages of interacting species (community modules or motifs) has significantly improved our understanding of the emergent properties of ecological communities. It is not clear whether all interactions accounted for in such models will be realized in real communities.
2. Here, we use community modules to experimentally explore whether the number of trophic links among species scales with community complexity (i.e., by adding species known to feed on each other from pair-wise trials) in a simple mite community present in avocado orchards (*Persea americana*). By varying the presence of each of two predators (*Euseius stipulatus* and *Neoseiulus californicus*), one herbivore as shared prey (*Oligonychus perseae*), and pollen of *Carpobrotus edulis* as an alternative food resource, we mimicked communities with simple trophic chains, intraguild predation and/or apparent competition. We then assessed predation rates and the conversion of food into offspring in those communities.
3. We found that increasing the number of potential interactions did not result in more complex realized community modules. Instead, all species effectively fed upon a single food item, hence all communities modules actually corresponded to one or two linear trophic chains.
4. Therefore, trophic links assumed to occur when species are assembled in pairs do not necessarily occur when other components of the community are present. Consequently, food-web structure may be much less complex than predicted by theory.

Key words:

Trophic interactions, pairwise interactions, community structure, intraguild predation, predatory mites

Introduction

Community ecology initially conceptualized trophic interactions as linear chains, with an upper level potentially controlling the densities of the level immediately below, thus generating a trophic cascade (Hairston *et al.* 1960; Oksanen *et al.* 1981). However, it is now accepted that most communities do not follow this pattern as organisms are embedded in complex food webs, blurring the notion of a trophic guild (*sensu* trophic coherence, Johnson *et al*. 2014) and questioning the prediction that widespread omnivory destabilizes food webs (Polis & Holt 1992; Polis & Strong 1996).

Food webs can be decomposed into "community modules" (Holt 1997) or motifs (Bascompte & Melián 2005; Prill *et al*. 2005), i.e. a small number of species (e.g. three to six) linked in a specified structure of interactions. Among those, intraguild predation (IGP), in which two consumers (the intraguild predator and the intraguild prey, hereafter IG-predator and IG-prey) not only compete for a shared resource but also engage in predator-prey interactions (Polis *et al.* 1989), and apparent competition, in which two non-competing prey share a common predator (Holt 1977; 1997), are the most common (Bascompte & Melián 2005). Whether and how often species engage in intraguild predation or apparent competition strongly affects the long-term persistence of communities (i.e., the "temporal stability in community composition", Pimm 1984). Theory predicts that intraguild predation destabilizes communities because it reduces the parameter space where coexistence of the IG-predator, IG-prey and shared prey is possible (Holt & Polis 1997), compared to that of a predator, a prey and a resource in trophic chain models (Oksanen *et al.* 1981). Some theoretical studies predict that the inclusion of some factors may reduce this instability (reviewed in Novak 2013, appendix S1). Such factors include habitat structure (Janssen *et al.* 2007), temporal (Amarasekare 2008) or developmental stage refuges (Mylius *et al.* 2001; Rudolf & Armstrong 2008), or the presence of alternative food (Faria & Costa 2010). These factors promote coexistence by bringing the community structure closer to two linear food chains. Thus, a prevailing outcome of the ecological theory is that domains of persistence of communities with IGP increase as the strength of trophic interactions between predator species decreases. Indeed, weak interactions have long been recognized to stabilize ecosystems by dampening oscillations between consumers and resources, thus promoting community persistence (McCann *et al.* 1998; Gellner & McCann 2016).

As communities become more complex, predator species can interact trophically with a higher number of potential prey. Community network building is typically done using the species fundamental trophic niches, which includes all the pairwise trophic interactions that this focal species can establish with others. However, it is known that the number of potential interactions in food webs tends to become much higher than the number of realized interactions (Beckermann *et al.* 2006). The factors affecting the ratio between who can eat whom and who actually eats whom (i.e., connectance) are similar to those leading to reduced IGP. Indeed, a few studies indicate that connectance is linked to structure of the habitats in which communities occur (Beckermann 2006, Tylianakis *et al.* 2007). Others show that connectance is best explained by the intrinsic value of food items. For example, wide differences in resource quality are predicted to decrease connectance (Beckermann *et al.* 2006). Similarly, flexible foraging behaviour may decrease connectance when food web complexity increases. This was elegantly shown in a study that compared several plant-pollinator interaction networks differing in size (Spiesman & Gratton 2016). The authors found that niche partitioning was stronger (ergo connectance was weaker) in highly diverse networks (i.e. networks with more plants and, thus, with more interspecific competitors) likely because pollinators adjusted their foraging strategies to minimize interspecific competition. Therefore, it is becoming clear that the fundamental trophic niches of species (i.e., with all their potential interactions; Elton 1927) may not always be realized (Hutchinson 1957).

Here, we test whether fundamental and realized trophic niches of species concur, by exploring, in a simple community, how pairwise trophic interactions between species are modified by the inclusion of other species. We focus on *predation rate* (here, number of individuals consumed per day) as a proxy for trophic interaction strength. Specifically, we mimicked different community modules of increasing complexity using a community composed of two predatory mite species (*Euseius stipulatus* and *Neoseiulus californicus*, Acari: Phytoseiidae), one herbivore mite species as their prey (*Oligonychus perseae*, Acari: Tetranychidae), and pollen as alternative food (González-Fernández *et al.* 2009), all of which inhabit avocado plants (*Persea americana*) in Southeastern Spain (Figure 1A). Previous pairwise experimental studies showed that the interaction between *N. californicus* and *O. perseae* is stronger (i.e., predation rates are higher) than that between *E. stipulatus* and this same prey (González-Fernández et al. 2009). Moreover, pollen is an optimal food source for

E. stipulatus but not for *N. californicus* (González-Fernández et al. 2009). Finally, *E. stipulatus* and *N. californicus* engage in size-dependent predator-prey interactions (Abad-Moyano *et al.* 2010). This knowledge was used to generate predictions on realized trophic links occurring in this system across community modules of increasing complexity (Figure 1B). These predictions were then tested through a series of experimental treatments to assess a) whether (IG-)predators feed on each prey type; b) whether predation of (IG-)predators on one prey type is affected by the presence of the other; c) whether predation of (IG-)predators on both prey, and of IG-prey on the herbivore, is affected by the presence of alternative food; and d) whether the presence of alternative food affects predation of (IG-)predators on the two types of prey when they are together. With this set of experimental treatments specific planned comparisons allowed unravelling which trophic interactions within each community module were realized, thus providing a relatively simple test of how realized trophic niches can be narrower than fundamental trophic niches when network complexity increases.

Material and Methods

All cultures and experiments were done in a climate chamber at 25±1ºC, 65±5% RH and 16:8h L:D (Light:Dark).

Mite cultures:

Cultures of the predatory mite *E. stipulatus* were started in 2007 from ca. 300 individuals collected from avocado trees located in the IHSM "La Mayora". Populations were kept on bean (*Phaseolus vulgaris* L.) plants, and mites were fed *ad libitum* twice a week with pollen of *Carpobrotus edulis* (cat's claw) spread on leaves with a fine brush. The *N. californicus* population was obtained from Koppert Biological Systems S.L. in bottles of 1000 individuals (Spical®). Colonies were kept on detached bean leaves infested with *Tetranychus urticae* that were placed on top of inverted flower-pots (20 cm Ø) inside water-containing trays. The herbivore *O. perseae* was not maintained in a laboratory culture due to technical difficulties in preserving detached avocado leaves. They were thus collected from the field on a regular basis from avocado orchards located in the IHSM "La Mayora". Pollen of *C.*

edulis was obtained from flowers collected in the experimental station. Stamens were dried in a stove at 37ºC for 48h, then sieved (350 µm).

Community modules

Experimental arenas to test the outcome of community modules have been described in detail in Guzmán *et al.* (2016). Briefly, a hole (6.5 cm Ø) was cut in a petri dish (9 cm Ø), turned upside down, and then filled with an avocado leaf disc (7.5 cm Ø). The borders were glued to a clay ring. Inside the petri dish, wet cotton wool ensured enough humidity to keep leaves turgid. Petri dishes were then sealed with parafilm®. To prevent individuals from escaping, a ring of Tanglefoot® was applied along the outer margin of the leaf disc.

We performed experiments using two *community blocks*, acording to the identity of the top predator or IG-predator (Figure 1). Because IGP interactions are size-dependent, IG-predators and IG-prey consisted of adult gravid females (10-14 days old after egg hatching) and heterospecific juveniles (2-3 days old since hatching), respectively. Individuals of known age were obtained from cohorts prepared prior to the start of the experiments. Throughout the text, the identity of (IG)-predator and (IG)-prey will be indicated using the subscripts "ES" for *E. stipulatus* and "NC" for *N. californicus*. Predator females were randomly taken from these cohorts, and starved for 16 h, to standardize hunger levels among individuals, and to ensure that egg production in tested females was not obtained from food ingested prior to the experiment. Arenas containing the herbivore were established as follows: Ten females of *O. perseae* were let to build nests and lay eggs on experimental arenas during 4 days. The number of nests and eggs per nest on each arena was counted at the onset of the experiment. Pollen in arenas assigned to treatments with alternative food was supplied *ad libitum*, using a fine brush.

Increased complexity was mimicked through the combination of the presence/absence of 4 trophic positions: (IG-)predator, IG-prey, herbivore and alternative food. This resulted in the community modules (Sensu Holt 1997) depicted in the X-axis of figures 2 and 3. These modules were: 1. Trophic chain: either one *E. stipulatus* or *N. californicus* female was introduced in arenas containing 10 *O. perseae* females (treatment # 1 in Figs 2 and 3). Arenas containing either one *E. stipulatus* or one *N. californicus* female without herbivores (treatment # 2), and others containing 10 *O. perseae* females without predators (treatment # 3) were done as controls for predator oviposition rate and prey

natural mortality, respectively. 2. Apparent competition: arenas consisted of one female of either *E. stipulatus* or *N. californicus*, 10 *O. perseae* females, and pollen of *C. edulis* supplied *ad libitum* (treatment # 4). Similar arenas but without herbivores (treatment # 5) were made as controls for oviposition rates of predators on pollen only, and without the IG-predator (treatment # 6) to assess potential effects of pollen on the survival of the herbivore. 3. Intraguild predation: Arenas consisted of 10 *O. perseae* females, either one *E. stipulatus* or *N. californicus* female, as IG-predators, and 10 heterospecific juveniles, as IG-prey (treatment # 7). Control treatments were done to evaluate: the predation/mortality rate of *O. perseae* in the presence of IG-prey but not of IG-predator (treatment # 8); the mortality rate of IG-prey in the absence of both IG-predator and prey (treatment # 9), and in the presence of IG-predator but not of herbivores (treatment # 10). 4. Intraguild predation - Apparent competition: Arenas consisted of 10 *O. perseae* females, either one *E. stipulatus* or *N. californicus* female, 10 heterospecific juveniles, and pollen of *C. edulis* as alternative food, supplied *ad libitum* (treatment # 11). Similar arenas to those above but i) without IG-predators (treatment # 12), ii) without herbivores (treatment # 13), and iii) without IG-predators and herbivores (treatment # 14), were done to evaluate predation of IG-prey on the herbivore in the presence of pollen, predation of IG-predators on IG-prey in the presence of pollen, and mortality of IG-prey in the presence of pollen, respectively.

Twenty-four hours later, the number of dead herbivores/IG-prey (predation/mortality rate), and the number of eggs laid by predators/IG-predators (oviposition rate) were recorded. Each treatment was replicated 10 to 18 times.

Data analyses

Statistical analyses were performed using the computer environment R (R Core Team 2017). Analyses were done separately for each *community block*. The effects of the presence/absence of each of the trophic groups in the community module, as well as the presence of alternative food on predation rates on herbivores and on IG-prey, and rates of oviposition of IG-predators, were analysed using Generalized Lineal Models (GLM) assuming a Poisson distribution and a Log-link function, as no overdispersion of the data was detected. All the analyses assumed 3 full-factorial designs and followed a backward elimination procedure: when the interaction among the three explanatory variables was not significant and the model had higher or not a substantially smaller AIC (i.e., by at least two

units) than that without the interaction, the latter was removed from the model. Subsequently, the same procedure was followed for second-order interactions, keeping as final model that with only significant interactions or no interactions at all (additive model). Using the significant terms of the above general models we performed a series of planned comparisons using the "contrast" R package, to detect the presence or absence of specific trophic links based on the patterns of mortality in the herbivore and the IGP-prey and on the oviposition rates of the IG-predator. When specific sets of data were used in multiple comparisons, their significance was corrected using the sequential Bonferroni method correction (Holm 1979, Rice 1989). Alfha levels after Bonferroni correction are indicated in the text as α_{Bonf}.

Mortality of *O. perseae* females was analysed using data from treatments containing this species. The 3 main factors in the model were presence/absence of IG-predators, IG-prey, and alternative food.

IG-prey mortality was analysed using data from treatments containing IG-prey (i.e. predator juveniles). The 3 main factors in the model were presence/absence of IG-predators, herbivores, and alternative food.

Oviposition rates were analysed using data from treatments containing IG-predators (i.e., adult predators). The 3 main factors in the model were presence/absence of herbivores, IG prey, and alternative food.

Results

Community block with E. stipulatus as the (IG-)predator

Mortality rates of the herbivore were significantly affected by the interaction between the presence of IG-predator$_{ES}$ and IG-prey$_{NC}$ and between the presence of IG-prey$_{NC}$ and pollen (Table 1a). Indeed, more prey died in arenas with both the IG-prey$_{NC}$ and the IG-predator$_{ES}$ than with the IG-predator$_{ES}$ alone (Fig 2a, compare bar 1 to 7), but not than with the IG-prey$_{NC}$ alone (Fig 2a, compare bar 8 to bar 7). Also, the presence of pollen led to reduced herbivore mortality rates, but only in the absence of IG-prey$_{NC}$ (Fig 2a, compare bars 4 and 6 to bars 11 and 12), suggesting that IG-prey$_{NC}$ were not feeding on pollen in the presence of herbivores and that the IG-predator$_{ES}$ stopped feeding on herbivores when pollen was present.

Mortality rates of the IG-prey$_{NC}$ were affected by all the double interactions except that between the herbivore and pollen (Table 1b). The presence of the IG-predator$_{ES}$ led to increased mortality of IG-prey$_{NC}$, but only in the absence of pollen (Fig 2b, compare bars 7 and 10 to bars 11 and 13), indicating that IG-predator$_{ES}$ tended not to feed on IG-prey$_{NC}$ if pollen was available. Similarly, the presence of herbivores led to reduced mortality rates of IG-prey$_{NC}$ in absence of IG-predators$_{ES}$ (Fig 2b, compare bar 8 to 9), but not in their presence (Fig 2b, compare bar 7 to 10), suggesting that IG-predators$_{ES}$ fed mostly on IG-prey$_{NC}$.

Planned comparisons revealed that a) IG-predators$_{ES}$ preyed on *O. perseae* [t_{81} = 2.74, P = 0.0076 (α_{Bonf} < 0.025); Fig 2a, compare bars 1 and 3] when the herbivore was offered alone ; b) adding IG-prey$_{NC}$ increased mortality of *O. perseae* (t_{81} = -2.26, P = 0.026 (α_{Bonf} < 0.05); Fig 2a, compare bar 1 to 7), while adding *O. perseae* did not influence mortality of the IG-prey$_{NC}$ (t_{80} = -0.31, P = 0.755 (α_{Bonf} < 0.05) Fig 2b, compare bar 10 to 7), indicating that IG-prey$_{NC}$ were feeding on the herbivore and that the IG-predator$_{ES}$ were mostly feeding on the IG-prey; c) the presence of pollen yielded a drastic reduction in predation of IG-predators$_{ES}$ on both the herbivore (t_{81} = 2.99, P = 0.0037 (α_{Bonf} < 0.017); Fig 2a, compare bar 1 to 4) and the IG-prey$_{NC}$ (t_{80} = 3.91, P << 0.001 (α_{Bonf} < 0.017); Fig 2b, compare bar 10 to 13), indicating that IG-predators$_{ES}$ were mostly feeding on pollen; d) when both prey were available, the presence of pollen did not affect herbivore mortality (t_{81} = 0.88, P = 0.379; Fig 2a, compare bar 7 to 11), but led to lower IG-prey$_{NC}$ mortality (t_{80} = 3.58, P << 0.001; Fig 2b, compare bar 7 to 11), suggesting that IG-prey$_{NC}$ were feeding on herbivores while the IG-predator$_{ES}$ fed mostly on pollen.

Oviposition rates of IG-predators$_{ES}$ were only affected by the presence of pollen (main factor Pollen, Table 1c) and indeed treatments with pollen resulted in much higher oviposition than those without pollen (compare bars 4, 5, 11 and 13 to bars 1, 2 , 7 and 10).

Community block with N. californicus as the (IG-)predator

Herbivore mortality was affected only by the interaction between IG-predator$_{NC}$ and IG-prey$_{ES}$ (Table 2a). Indeed, mortality of herbivores was drastically affected by the presence of IG-predators$_{NC}$ (Fig 3a, compare bar 1 to 3), but this effect was lower in the additional presence of IG-prey$_{ES}$ (Fig 3a, compare bar 1 to 7). Mortality of IG-prey$_{ES}$ was only affected by the presence of pollen (Table 2b).

Paired comparisons revealed that a) IG-predators$_{NC}$ preyed on *O. perseae* (t_{90} = 3.32, P = 0.013 (α_{Bonf} < 0.025); Fig 3a, compare bar 3 to 1) but not on IG-prey$_{ES}$ (t_{86} = -1.35, P = 0.182 (α_{Bonf} < 0.025); Fig 3b, compare bar 9 to 10), when each prey was offered alone; b) adding IG-prey$_{ES}$ reduced mortality of *O. perseae* (t_{90} = 2.56, P = 0.012 (α_{Bonf} < 0.017); Fig 3a, compare bar 1 to 7), but adding *O. perseae* did not change mortality of the IG-prey$_{ES}$ (t_{86} = -0.93, P = 0.353 (α_{Bonf} < 0.05); Fig 3b, compare bar 10 to 7); c) the presence of pollen did not affect mortality of either *O. perseae* (t_{90} = -0.43, P = 0.669 (α_{Bonf} < 0.05); Fig 3a, compare bar 1 to 4) or the IG-prey$_{ES}$ (t_{86} = 1.80, P = 0.075 (α_{Bonf} < 0.017); Fig 3b, compare bar 10 to 13) when they were alone with the IG-predator$_{NC}$; d) when both types of prey were present with the IGP-predator$_{NC}$, the presence of pollen led to a significant increase in mortality of *O.perseae* (t_{90} = -3.65, P << 0.001; Fig 3a, compare bar 7 to 11), but a significant decrease of mortality in IG-prey$_{ES}$ (t_{86} = 2.04, P = 0.044; Fig 3b, compare bar 7 to 11).

Oviposition rates of IG-predators$_{NC}$ were affected by the main factor Herbivore and the interaction between the IG-prey$_{ES}$ and pollen (Table 2c). Indeed, paired comparisons revealed that eggs were produced when IG-predators$_{NC}$ were offered the herbivore alone (t_{104} = 2.45, P = 0.016 (α_{Bonf} < 0.017); Fig 3c, compare bar 1 to 2), but not when they were on arenas with either the IG-prey$_{ES}$ (t_{104} = 0.01, P = 0.992 (α_{Bonf} < 0.05); Fig 3c, compare bar 10 to 2) or pollen (t_{104} = -0.15, P = 0.884 (α_{Bonf} < 0.025); Fig 3c, compare bar 5 to 2) alone. Moreover, in presence of the herbivore, rates of oviposition were not influenced by the presence of pollen (t_{104} = -0.93, P = 0.352 (α_{Bonf} < 0.05); Fig 3c, compare bar 1 to 4), but dramatically decreased in the presence of the IG-prey$_{ES}$ (t_{104} = 2.39, P = 0.019 (α_{Bonf} < 0.025); Fig 3c, compare bar 1 to 7). However, when pollen was added to the system with both prey types, IG-predators$_{NC}$ resumed oviposition to its maximum (t_{104} = -2.36, P = 0.020 (α_{Bonf} < 0.05); Fig 3c, compare bar 7 to 11).

Realized trophic interactions

a) Trophic chain: Comparisons between bars 1 and 3 in figures 2a and 3a confirmed that trophic links between both species of predator mite and the herbivore were realized (figure 1, a.2.1 and a.2.2), and that trophic interactions translated into predator fecundity (compare columns 1 and 2 in figures 2c and 3c).
b) Apparent competition: When pollen was added to the trophic chain community module, *E. stipulatus* ceased preying on the herbivore (compare bars 1 and 4, figure

2a), and foraged exclusively on pollen (compare bars 4 and 5 in figure 2c). This resulted in the realized food web configuration depicted in figure 1, b.2.1. In contrast, *N. californicus* kept foraging on the herbivore (compare bars 1 and 4, figure 3a), and not on pollen, as it is pointed by the lack of food conversion into eggs (compare bars 4 and 5, and 4 and 1, in figure 3c). This resulted in the realized food web configuration depicted in figure 1, b.2.2.

c) Intraguild predation: When intraguild prey was added to the trophic chain community, *E. stipulatus* preyed on the IG-prey (compare bars 7 and 8, figure 2b), but not on the herbivore: bars 7 and 8 in figure 2a indicate that mortality of the herbivore was inflicted by the IG-prey$_{NC}$, which is supported by comparing oviposition rates of the IG-predator$_{ES}$ with and without IG-prey (bars 1 and 7, figure 2c). This resulted in the realized food web configuration depicted in figure 1, c.2.1. In the presence of the IG-prey$_{ES}$, *N. californicus* ceased foraging on the herbivore (compare bars 1 and 7, figure 3a), which translated into no predator fecundity (compare bars 1 and 7, figure 3c). Instead, herbivore mortality was inflicted by the IG-prey$_{ES}$ (compare bars 7 and 8, figure 3a). This resulted in the realized food web configuration depicted in figure 1, c.2.2.

d) Intraguild predation and apparent competition: when pollen was added to the IGP community module with *E. stipulatus* as the IG-predator, herbivore mortality was mainly inflicted by the IG-prey$_{NC}$ (compare bars 11 and 12, figure 2a). IG-predators$_{ES}$ ceased attacking the IG-prey$_{NC}$ (compare bars 7 and 11, figure 2b) and foraged exclusively on pollen, its optimal food (compare oviposition rates, bars 7 and 11, and bars 5 and 11, figure 2c). This resulted in the realized food web configuration depicted in figure 1, d.2.1. Adding pollen to the IGP community module with *N. califonicus* as the IG-predator resulted in the latter attacking herbivores [compare bars 7 and 11 in figure 3a (predation rates) and in figure 3c (oviposition rates)], and on the survival of IG-prey$_{ES}$ increasing in the presence of its optimal food (compare bars 7 and 11 in figure 3b). This resulted in the realized food web configuration depicted in figure 1, d.2.2.

Discussion

In this study, we tested the effect of community structure on the realized interactions within a community of predatory and herbivorous mites. We show that adding species to a community increases the number of potential trophic interactions, but not necessarily their occurrence. Indeed, despite the potential for module configurations of communities with apparent competition and intraguild predation, all modules could be described by linear food chains in our system (Figure 1C).

Basic properties of the experimental system and implications for population dynamics

All the community modules considered in this study naturally occur in the avocado orchards of South-eastern Spain. Field samplings done on avocado trees during four consecutive years revealed that the population dynamics of phytoseiids typically has two maxima, one in spring and the other in summer. In spring, the phytoseiid population growth is strongly linked to the dynamics of pollen concentration in the atmosphere (Montserrat *et al.* 2013). Atmospheric pollen (mostly from olive trees) deposits on the surface of avocado leaves and becomes a food source for *E. stipulatus*, the most abundant mite predator in spring (81 %) (González-Fernández *et al.* 2009). In summer, phytoseiid populations respond numerically to the exponential growth of the persea mite (Montserrat *et al.* 2013). At this time, *N. californicus* and *E. stipulatus* are by far the two most abundant phytoseiid mite species (50% and 34%, respectively). The results here contribute to explain the community dynamics observed in the field:

In the trophic chain configurations, *N. californicus* killed more *O. perseae* females per day than *E. stipulatus*, yet oviposition rates were similar between predators. Indeed, *E. stipulatus* can only forage on mobile *O. perseae* mites when they wander outside nests, whereas *N. californicus* can penetrate inside nests and forage on all the individuals residing within (González-Fernández *et al.* 2009). This suggests that *E. stipulatus* is the most efficient predator converting food into eggs, but that *N. californicus* is more efficient at reducing herbivore populations. Moreover, unlike *N. californicus*, *E. stipulatus* fed and oviposited on pollen. This allows the latter to remain in the field when animal prey is scarce, as observed in field surveys in springtime (González-Fernández *et al.* 2009).

Our results also revealed asymmetry in intraguild predation between *E. stipulatus* and *N. californicus*, with adults of the former preying upon juveniles of the latter, but not

the reverse. Because *N. californicus* is likely the best competitor for the shared prey, coexistence between predators is thus possible in this system (Holt & Polis 1997). Yet, the simultaneous presence of the two predators is likely to have little effect upon the densities of the shared prey. Indeed, whereas adding *N. californicus* adults to an arena with *E. stipulatus* juveniles results in higher shared prey densities as compared to the presence of *N. californicus* adults alone with the shared prey, the reverse is not true when adding adult *E. stipulatus* to an arena with juveniles *N. californicus*. Thus, the net effect of these interactions upon prey density is probably negligible. This is corroborated by field studies showing that natural population control of the persea mite when the two species of predators are present is not successful (Montserrat *et al.* 2013). However, the presence of alternative food (i.e. pollen) contributed to reduce trophic interactions between predator species resulting in community configurations that could enhance pest control. Thus, supplying alternative and preferred food to the IG-predator is probably detrimental to populations of *O. perseae*. Again, this finding is in line with field observations (Montserrat *et al.* 2013). In this work, the authors spread commercial bee pollen dissolved on water onto the avocado trees, resulting on a better control of *O. perseae* populations.

Optimal foraging theory predicts that species engage in trophic interactions on more than one food source when these are available (Pulliam 1974). Here, we show that *E. stipulatus* acting as intraguild predators feeds on the herbivore, *O. perseae*, on the intraguild prey, *N. californicus*, and on the alternative food, pollen, when each of these are presented alone. However, in the presence of pollen, *E. stipulatus* stops feeding on both prey species. This may be explained by the fact that pollen is the most profitable food for this species (Ferragut *et al.* 1987). Similarly, *N. californicus* adults and juveniles ceased foraging on other food sources in presence of the herbivore. These results suggest that realized interactions hinge on the presence of the most profitable food source. Indeed, in the most complex community studied here, with all 5 species present, the presence of the optimal food source for each predator species originated the split of the community into two trophic chains, one with *E. stipulatus* feeding on pollen and the other with *N. californicus* feeding on the herbivore (Figure 1 d).

Another factor that contributed to the linearization of the food web was that, when both the IG-prey and the shared prey were together, IG-predators$_{ES}$ preyed mainly on the IG-prey$_{NC}$. Indeed, mortality of *O. perseae* in presence of juvenile *N. californicus*, was not

affected by the presence of the adult *E. stipulatus*. Furthermore, mortality of IG-prey$_{NC}$ was significantly higher in treatments with IG-predators$_{ES}$, compared to controls without them. This suggests that mortality in the herbivore was mainly inflicted by the IG-prey$_{NC}$, and that the IG-predator$_{ES}$ preyed preferentially on the IG-prey$_{NC}$. This could be explained by *E. stipulatus* having no access to herbivore prey located inside the nests, which leads to higher encounter rates between IG-predator$_{ES}$ and IG-prey$_{NS}$ than between IG-predator$_{ES}$ and herbivores. Indeed, *E. stipulatus* forages only on mobile stages that wander outside nests whereas *N. californicus* can penetrate *O. perseae* nests, and thus may feed on them (González-Fernández *et al.* 2009). Therefore, the realized community was that of a 4-level trophic chain (Figure 1, c.2.1.). In the other community block, when *N. californicus* acted as the IG-predator, mortality of *O. perseae* females was similar in all communities with the IG-prey$_{ES}$ present, irrespective of the presence of IG-predators$_{NC}$. Furthermore, mortality of IG-prey$_{ES}$ did not differ between treatments with and without the IG-predator$_{NC}$, indicating that *N. californicus* females did not forage on *E. stipulatus* juveniles. These results suggest that, in presence of IG-prey$_{ES}$, the IG-predator$_{NC}$ ceased to forage on either herbivore or IG-prey$_{ES}$, likely because IG-prey$_{ES}$ interferes with the foraging activities of IG-predators$_{NC}$. Thus, the realized community was that of a trophic chain composed of the IG-prey, the herbivore and the plant, with the IG-predator not interacting at all (Figure 1, c.2.2.). This can be explained by IG-predators$_{NC}$ avoiding foraging on a patch where its offspring (future) IG-predator is also there. In any case, here, the trophic links are again linear, with *N. californicus* being excluded from the realized community (Figure 1, c.2.2.). Together, our results show that none of the complex communities was actually realized, they were all trophic chains.

The return of the trophic chain: **Fundamental vs realized trophic interactions**

By combining data of mortality and oviposition at different community structures, we could determine who eats whom in a simple food web. Although this approach is powerful, it does have its limitations. Indeed, it assumes additive effects of conversion efficiencies of pairwise interactions. For example, if feeding on a prey item allows predators to better convert the food provided by another prey, this cannot be detected in our approach. Furthermore, it may be largely unfeasible to extend this approach to more complex food webs. Indeed, these full-factorial studies are extremely rare in the literature (but see Schmitz & Sokol-Hessner 2002; Otto *et al.* 2008). Still, it is becoming clear that we

need to know how food is transformed into predator offspring in order to fully understand food webs in nature (Neutel & Thorne 2014).

Connectance is a fundamental measure of food-web complexity that describes the proportion of realized interactions amongst all possible ones (May 1972). Connectance is generally much lower than the number of potential interactions (Beckerman *et al.* 2006). Identifying trophic links in food webs, however, is not a simple task. Molecular methods are useful to process field data and they deliver reliable information on who eats whom, but such tools currently only provide semi-quantitative estimates of predation, and they are expensive (Birkhofer *et al.* 2017). Modelling complex systems provides relative estimates of interaction strengths that go beyond pair-wise interactions (Moya-Laraño *et al.* 2012; 2014), but they call for experimental validation. Also, some recent methodological studies suggest solutions to infer pairwise interactions from complex food webs (Pomeranz *et al.* 2018). Another possible approach to measure connectance is performing field observations (Dunne *et al.* 2002; Tylianakis *et al.* 2007; Carnicer *et al.* 2009; Lazzaro *et al.* 2009; Baiser *et al.* 2016; Lemos-Costa *et al.* 2016). Although this approach permits the inclusion of a high number of species, it suffers from two main shortfalls: (a) it is generally only possible to undertake in systems with two trophic levels in which one is composed of primary producers, for example in plant-pollinator networks (but see Bukovinszky *et al.* 2008; Neutel & Thorne 2014), or in systems where trophic interactions are detectable long after the actual events, as in parasitoid/host interactions; and (b) it does not account for how foraging on a given resource translates into consumer offspring (but see Bukovinszky *et al.* 2008; Vázquez *et al.* 2015). Observations in controlled experimental settings, in contrast, deliver quantitative estimates of predation rates and concomitant offspring production, especially when trophic links and their strength are estimated by confronting pairs of species. Yet, one-on-one approaches may ignore emergent indirect effects of having several species together (Wootton 1994). For instance, *Cancer productus*, a crab native to the Northwest Pacific, consumes equal amounts of native oysters and of invasive drill oysters when each type of prey is offered alone, but when these prey are offered together, crabs interact with the native oyster species only (Grason & Miner 2012). Therefore, if trophic links are not evaluated in presence of all species in the community, one may overestimate connectance in food webs. Here, we show that all communities ended up becoming a sum of one or more trophic chains (Figure 1C). Thus, the fundamental trophic niche of species in this system

(i.e., the food items that species are potentially able to feed on) is larger than the realized trophic niche [i.e., the food items that species actually feed on when present in combinations exceeding the individual pairwise interactions (Hutchinson 1961)]. This indicates that indirect interactions, such as IGP and apparent competition, may be weak or absent. Therefore, our results suggest that some food webs may be less complex than previously thought.

Theoretical models exploring persistence in communities with IGP find a limited parameter space for three-species coexistence (e.g. Mylius *et al.* 2001), but field observations show that IGP is actually widespread (Polis 1991). Our results suggest that IGP in some systems might actually be occasional, as predators will tend to forage on the most profitable food, which is generally not the IG prey (Polis *et al.* 1989). In line with this, some natural systems have shown that communities with IGP show dynamics that are compatible with linear food chains, rather than with IGP (Borer *et al.* 2003). Therefore, predators may coexist because they rarely engage in IGP, and complexity may be over-estimated (Magalhães *et al.* 2005). Alternatively, species persistence may be achieved because predators consume their preferred food when the latter is available, but may switch to less-preferred items when their preferred food is depleted (Wei 2019). This could well be the case in our system. Both these alternatives are compatible with food web theory stating that weak trophic interactions promote the persistence of communities (McCann *et al.* 1998; Gellner & McCann 2016, among others). Our results suggest that increasing the number of potentially interacting species results in most species interactions becoming weaker. Indeed, the structure of interactions among species in natural communities is characterized by many weak and few strong interactions (Paine 1992; McCann *et al.* 1998), and such skewedness towards weak interactions is crucial to food web persistence (Neutel *et al.* 2002; 2007).

Furthermore, trophic interaction strengths are unlikely to be constant over time. For example, seasonal changes in species composition cause temporal variation in the strength of interactions (Carnicer et al. 2009, Gabaldon et al. 2019, Wang et al 2019), as well as changes in food-web topology and structure (McLaughlin et al 2010). In agroecosystems, temporal variability in species interaction strength is detectable even within crop seasons, as recently shown by Roubinet *et al*. (2018) in a barley field. Therefore, because a species' fundamental trophic niche (all of its potential interactions) is unlikely to be realized at a

particular place or time, it is crucial to determine the resources which species in a community actually feed upon, and under what circumstances. Thus, unravelling realized food webs, (i.e., interaction strengths across different nodes and trophic levels, including indirect effects) may be key to understanding these ecological networks and their persistence.

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Table 1. Results of Generalized Linear Models applied to a) herbivore mortality rates, b) IG-prey (juveniles of *N. californicus*) mortality rates, and c) (IG-)predator (females of *E. stipulatus*) oviposition rates. All the analyses were 3 full-factorial designs. When interactions among the three explanatory variables were not significant, and if the new model yielded a lower AIC, they were removed from the model. Subsequently, the same procedure was followed for double interactions. These cases are shown in the table as NS*.

a)	Herbivore mortality rates	Estimate	Std. Error	z value	Pr(>|z|)
	Intercept	-1.755	0.712	-2.466	0.014
	IG-predator (1)	2.212	0.732	3.021	0.002
	IG-prey (2)	2.932	0.729	4.023	<0.001
	Pollen (3)	-1.851	0.609	-3.040	<0.001
	IG-predator * IG-prey	-2.302	0.756	-3.047	0.002
	IG-predator * Pollen	NS			
	IG-prey * Pollen	1.573	0.639	2.466	0.014
	(1) * (2) * (3)	NS			

b)	IG-prey mortality rates	Estimate	Std. Error	z value	Pr(>|z|)
	Intercept	0.513	0.238	2.156	0.031
	IG-predator (1)	0.591	0.273	2.163	0.030
	Herbivore (2)	-1.624	0.496	-3.276	0.001
	Pollen (3)	-0.392	0.359	-1.091	0.275
	IG-predator * Herbivore	1.552	0.511	3.037	0.002
	IG-predator * Pollen	-1.705	0.517	-3.300	<0.001
	Herbivore * Pollen	0.749	0.520	1.439	0.150
	(1) * (2) * (3)	NS			

c)	IG-predator oviposition rates	Estimate	Std. Error	z value	Pr(>|z|)
	Intercept	-0.843	0.245	-3.443	<0.001
	IG-prey (1)	-0.194	0.220	-0.882	0.378
	Herbivore (2)	0.220	0.216	1.018	0.308
	Pollen (3)	1.104	0.235	4.703	<0.001
	IG-prey * Herbivore	NS			
	IG-prey * Pollen	NS			
	Herbivore * Pollen	NS			
	(1) * (2) * (3)	NS*			

Table 2. Results of Generalized Linear Models applied to a) herbivore mortality rates, b) IG-prey (juveniles of *E. stipulatus*) mortality rates, and c) (IG-)predator (females of *N. californicus*) oviposition rates. All the analyses were 3 full-factorial designs. When interactions among the three explanatory variables were not significant, and if the new model yielded a lower AIC, they were removed from the model. Subsequently, the same procedure was followed for double interactions. These cases are shown in the table as NS*.

a)

Herbivore mortality rates	Estimate	Std. Error	z value	Pr(>|z|)
Intercept	-1.954	0.722	-2.707	0.007
IG-predator (1)	2.997	0.729	4.109	<0.001
IG-prey (2)	2.184	0.746	2.927	0.003
Pollen (3)	-0.888	0.499	-1.782	0.075
IG-predator * IG-prey	-2.825	0.764	-3.699	<0.001
IG-predator * Pollen	0.999	0.460	2.175	0.030
IG-prey * Pollen	0.791	0.325	2.436	0.015
(1) * (2) * (3)	NS*			

b)

IG-prey mortality rates	Estimate	Std. Error	z value	Pr(>|z|)
Intercept	-0.4855	0.3035	-1.600	0.110
IG-predator (1)	0.6150	0.3152	1.951	0.051
Herbivore (2)	-0.3174	0.2851	-1.114	0.265
Pollen (3)	-1.1505	0.3416	-3.368	<0.001
IG-predator * Herbivore	NS*			
IG-predator * Pollen	NS*			
Herbivore * Pollen	NS*			
(1) * (2) * (3)	NS*			

c)

IG-predator oviposition rates	Estimate	Std. Error	z value	Pr(>|z|)
Intercept	-2.7430	0.6172	-4.444	<0.001
IG-prey (1)	-2.5550	1.0378	-2.462	0.014
Herbivore (2)	2.5174	0.5989	4.204	<0.001
Pollen (3)	0.3476	0.3685	0.943	0.346
IG-prey * Herbivore	NS*			
IG-prey * Pollen	2.2175	1.1041	2.008	0.045
Herbivore * Pollen	NS*			
(1) * (2) * (3)	NS*			

Figure 1. **A: Fundamental community modules** included in this study. a) trophic chain, b) apparent competition, c) intraguild predation, and d) intraguild predation and apparent competition. From a) to d) the complexity of the community is increased via increasing the number of species and the number of interactions among them. **B: Predicted trophic links** that have been observed using pairwise experimental settings**. C: Realized trophic links** occurring across community modules of increasing complexity, obtained from the experiments presented here, where interactions are measured in the presence of other components of the community. SC stands for secondary consumer, PC for primary consumer, PP for primary producer, and AF for alternative food. SC1 and SC2 are phytoseiid predatory mites, i.e. *Euseius stipulatus* and *Neoseiulus californicus*, respectively, PC is the tetranychid herbivore mite *Oligonychus perseae*, AF is pollen of *Carpobrotus edulis*, and PP is the avocado *Persea americana*. Solid arrows indicate negative direct interactions (who eats whom), whereas dotted and dashed arrows in Figure 1A indicate negative indirect interactions (apparent competition and competition).

Figure 2. Mortality rates (average ± S.E.) of a) herbivore prey (*Oligonychus perseae* females) and b) IG-prey (*Neoseiulus californicus* juveniles), and c) oviposition rates (average ± S.E.) of IG-predators (*Euseius stipulatus* females), in 14 different treatments defined by presence or absence of either IG-predators, IG-prey, herbivores or alternative food (pollen), depicted in the lower part of the figure, that mimicked four different community configurations and their respective controls.

Figure 3. Mortality rates (average ± S.E.) of a) herbivore prey (*Oligonychus perseae* females) and b) IG-prey (*Euseius stipulatus* juveniles), and c) oviposition rates (average ± S.E.) of IG-predators (*Neoseiulus californicus* females), in 14 different treatments defined by presence or absence of either IG-predators, IG-prey, herbivores or alternative food (pollen), depicted in the lower part of the figure, that mimicked four different community configurations and their respective controls.

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Figure 1.

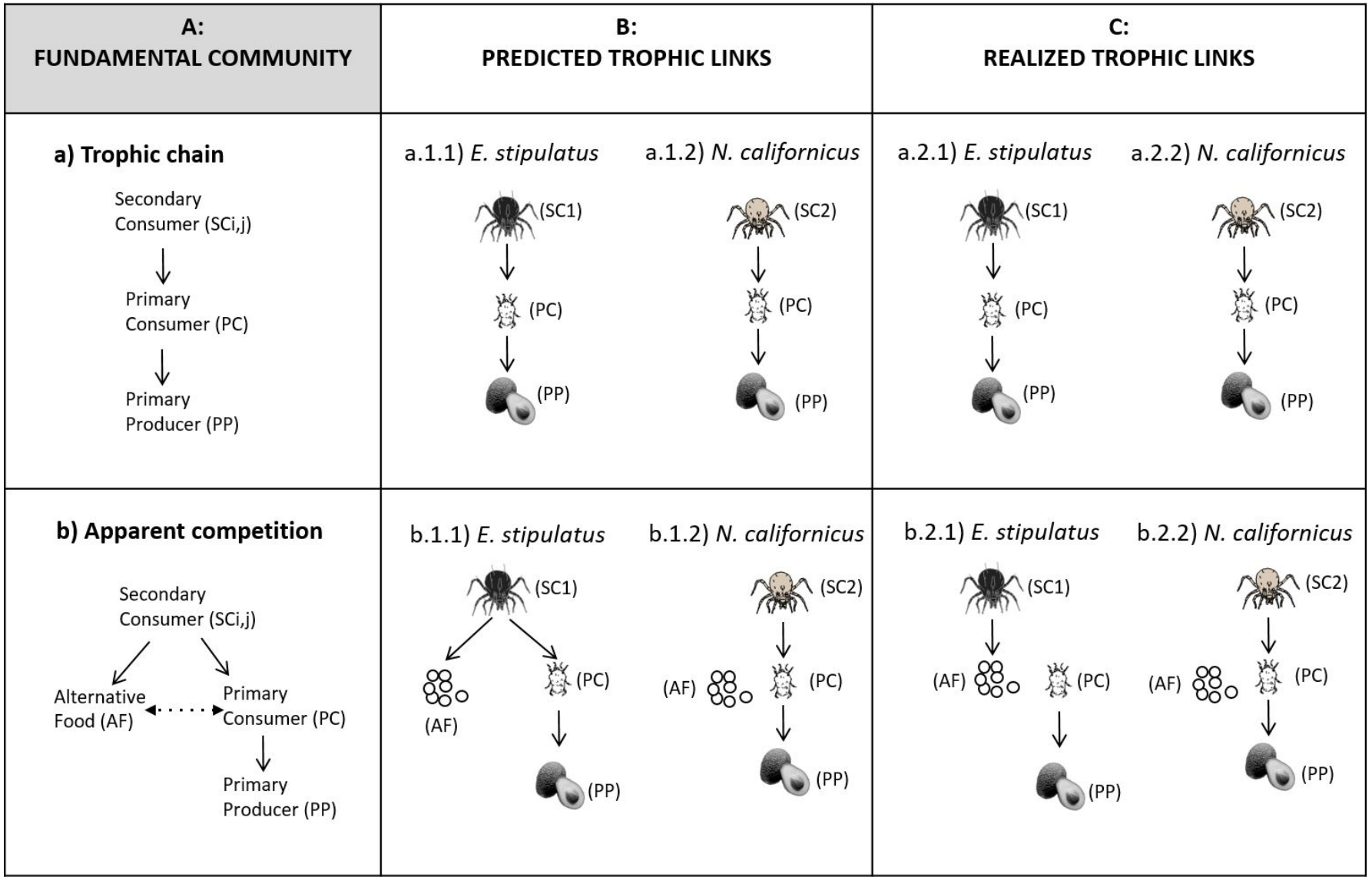
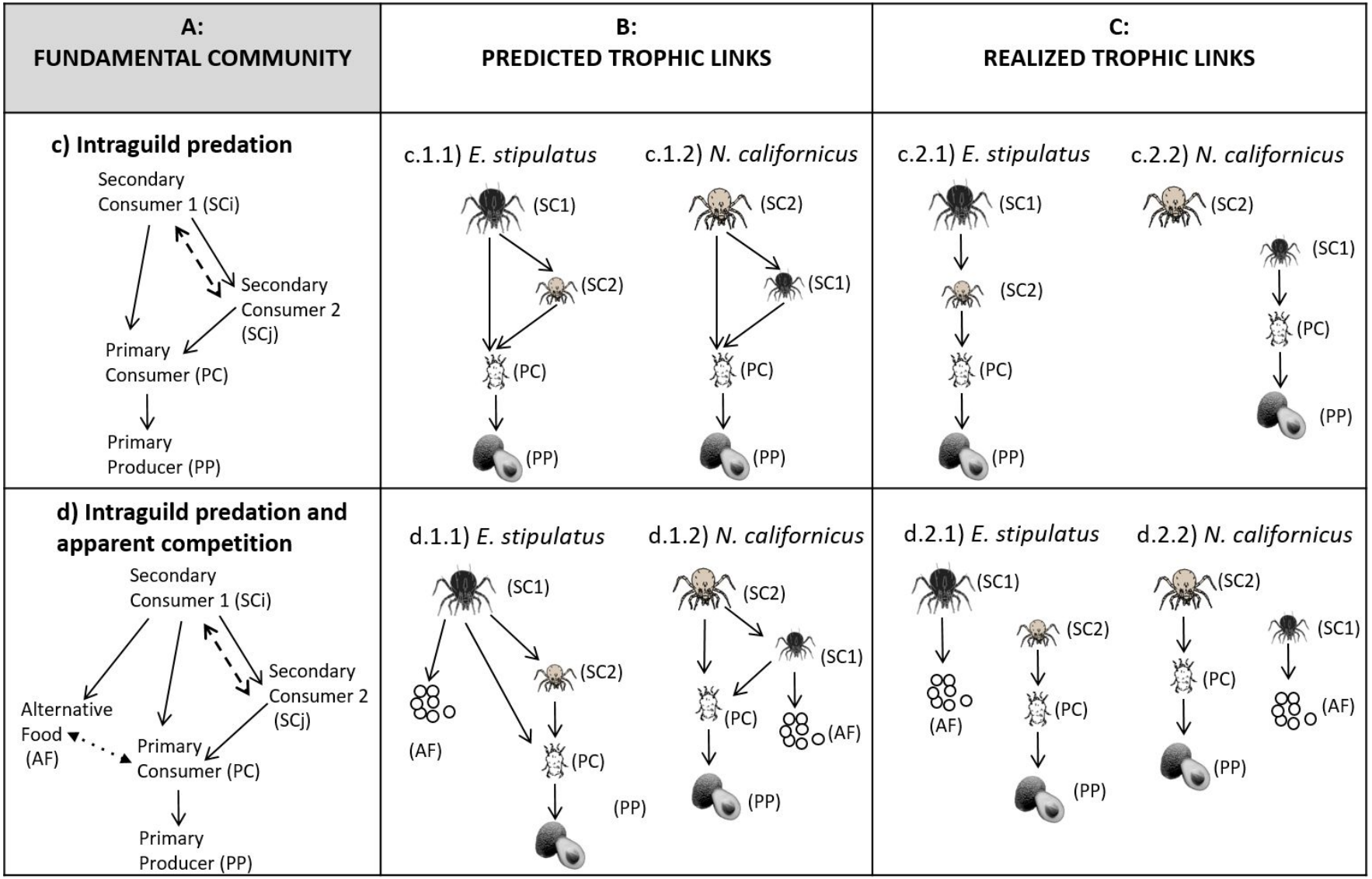
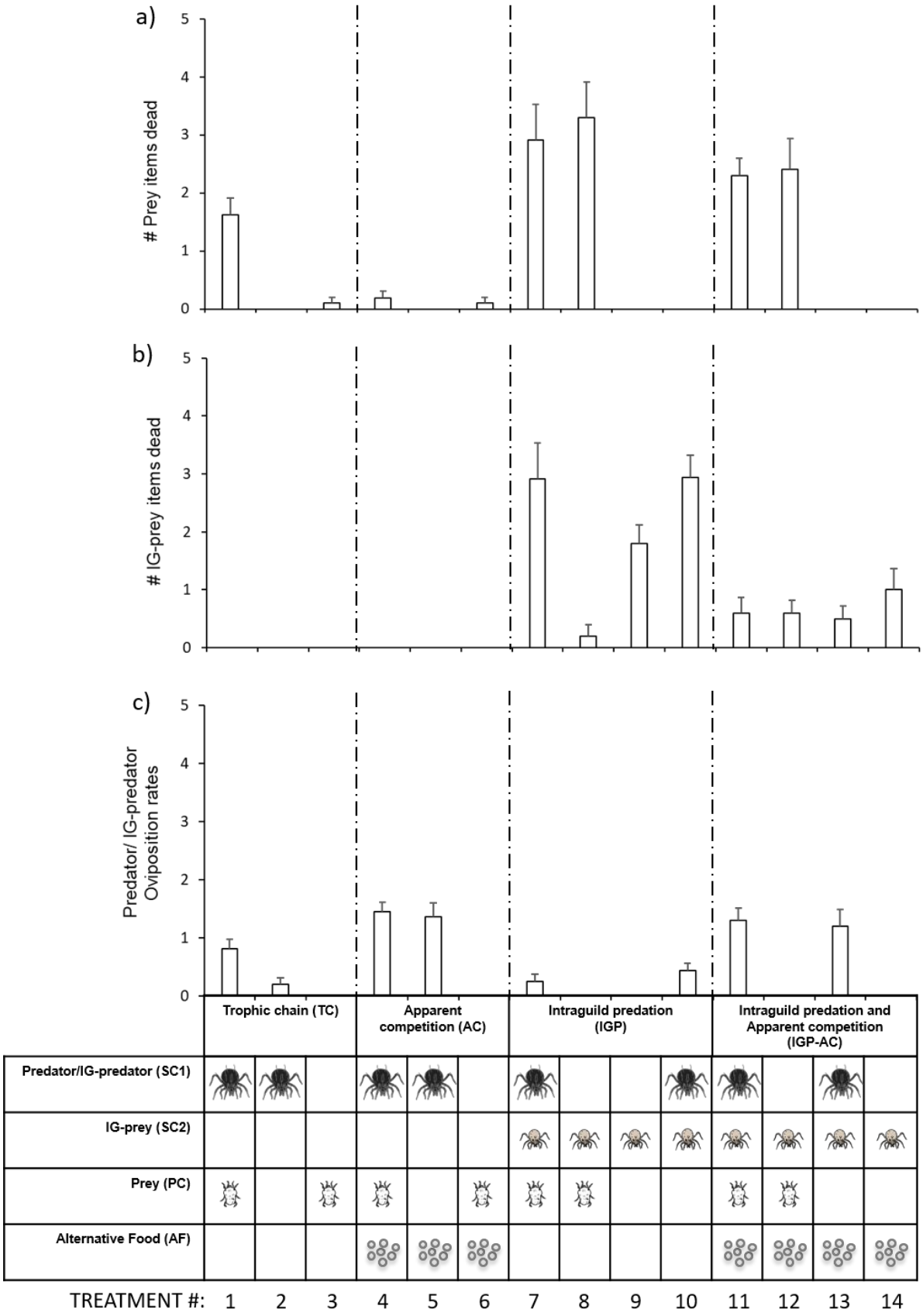

A:
FUNDAMENTAL COMMUNITY
B:
PREDICTED TROPHIC LINKS
C:
REALIZED TROPHIC LINKS
a) Trophic chain
Secondary Consumer (SCi,j)
Primary Consumer (PC)
Primary Producer (PP)
a.1.1) E. stipulatus
a.1.2) N. californicus
a.2.1) E. stipulatus
a.2.2) N. californicus
(SC1)
(SC2)
(PC)
(PP)
b) Apparent competition
Secondary Consumer (SCi,j)
Alternative Food (AF)
Primary Consumer (PC)
Primary Producer (PP)
b.1.1) E. stipulatus
b.1.2) N. californicus
b.2.1) E. stipulatus
b.2.2) N. californicus
(AF)

Figure 1 (cont.)



755 Figure 2.



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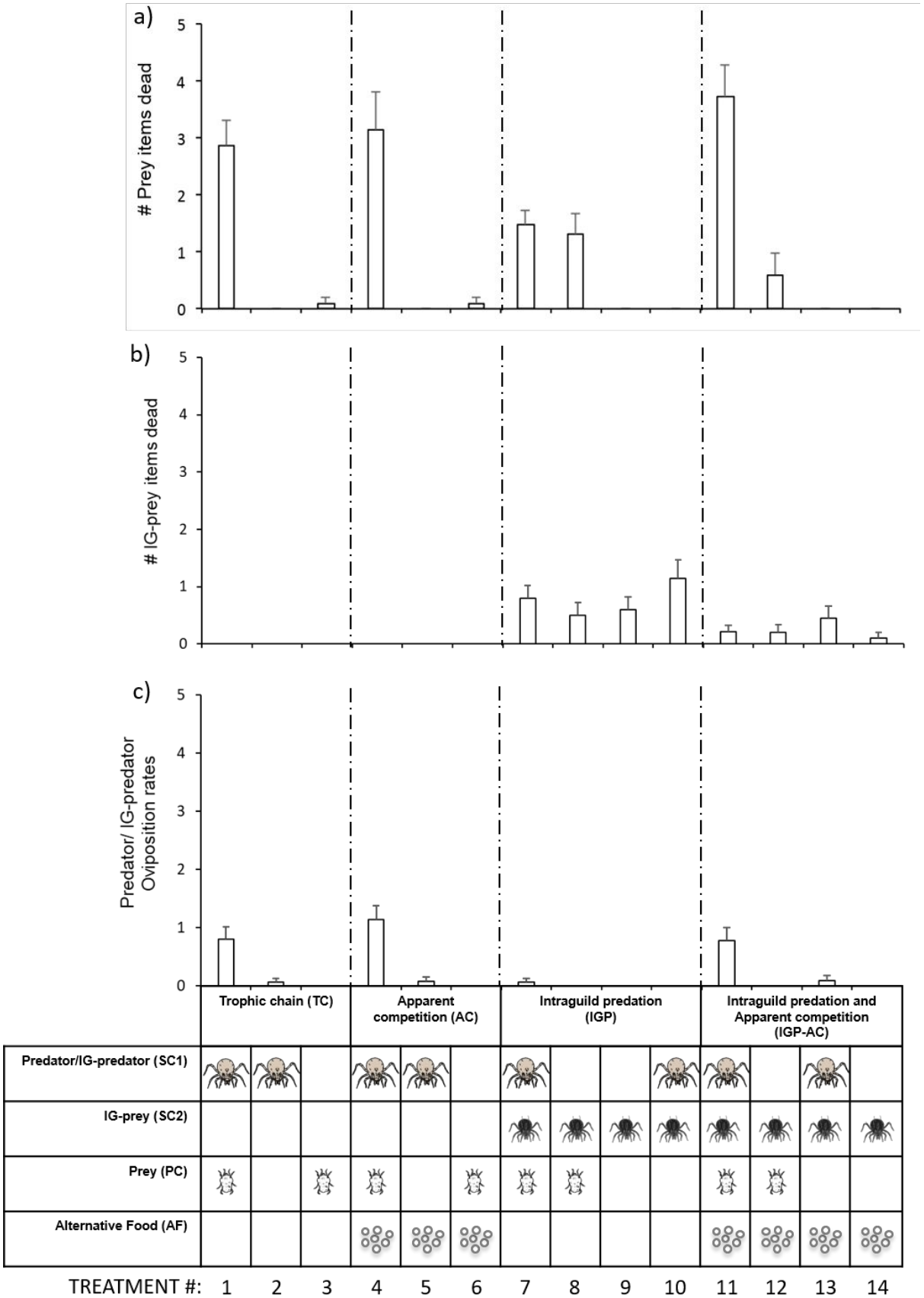
757 Figure 3.



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